

**The relative importance of aquatic and terrestrial variables for frogs in an urbanizing
landscape: Key insights for sustainable urban development**

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Abstract

Globally, urbanization threatens ~950 amphibian species with extinction. Yet a lack of knowledge on the factors influencing common and infrequently encountered species in landscapes that are under increasing pressure from urban development is limiting effective conservation. We examined the relative importance of aquatic variables (pond) and terrestrial variables (at three spatial scales: 10 m, 100 m and 1 km), for commonly and infrequently encountered frogs in an urbanizing forested landscape in southeastern Australia. Species richness and the occurrence of four common species were influenced by the aquatic environment (water body size, aquatic vegetation). Species richness also decreased with increasing urbanization within 1 km. This trend was driven by a strong decrease in richness of infrequently encountered species with increasing road length within 1 km from breeding ponds. Richness of infrequently encountered species also decreased with a reduction in forest cover within 10 m to 1 km from breeding ponds. Our findings suggest that frog conservation in urbanizing landscapes requires a mix of strategies across different spatial scales. Maintaining or re-establishing common frogs in urbanizing forested landscapes is likely to be achieved by providing ponds with suitable habitat. However, to conserve several frog species that are sensitive to forest loss and urbanization, breeding habitats need to be maintained within a network of large forest reserves.

Keywords: Common and rare species; *Crinia signifera*; *Litoria peronii*; *Limnodynastes peronii*; pond-breeding amphibians; forest-urban gradient.

1. Introduction

As the human population increases, a better understanding of how amphibian species respond to urbanization is needed worldwide. Urban human populations will increase by 2.7 billion from 2010 to 2050 (United Nations, 2012). Therefore, development for residential purposes will continue modifying landscapes and threatening biodiversity in many regions of the world (Beninde, Veith, & Hochkirch, 2015; McDonnell & Hahs, 2015; Villaseñor, Blanchard, & Lindenmayer, 2016). Among vertebrates, amphibians are the most threatened group: about 40% of amphibian species are threatened with extinction and the average size of populations has declined by up to 80% in the last four decades (based on 357 populations of 162 species from around the world; Baillie, Griffiths, Turvey, Loh, & Collen, 2010). Given that urban development threatens about 950 amphibian species with extinction (Baillie et al., 2010; Hamer & McDonnell, 2008), how can we conserve amphibians in an urbanizing world?

Amphibians rely on aquatic environments for breeding and larval development, and on terrestrial environments during juvenile and adult stages (Anstis, 2007; Semlitsch & Skelly, 2008). Thus, attributes of aquatic and terrestrial environments can affect amphibian distributions. Key variables from the aquatic environment influencing amphibian distributions include water body size, hydroperiod (i.e., period covered by water), the presence of fish and aquatic vegetation. Larger water bodies can support higher species richness (Parris, 2006). Hydroperiod can influence the species inhabiting a wetland (e.g., in ephemeral pools; Baldwin, Calhoun, & deMaynadier, 2006; Semlitsch, 2000). Predatory fish can have detrimental effects on amphibians

(Shulze, Semlitsch, & Trauth, 2013), whereas aquatic vegetation may provide refuge against predation during amphibian larval stages (Hamer & Parris, 2011).

Modification of terrestrial environments, such as clearing of vegetation for urban development, can lead to habitat loss and fragmentation (Hamer & McDonnell, 2008; Semlitsch & Skelly, 2008), and influence amphibian populations from local to landscape scales (Hamer & Parris, 2011). Important variables from the terrestrial environment influencing amphibian distribution include fringing vegetation (i.e., vegetation adjacent to waterbodies), as well as forest cover and urban infrastructure at different landscape scales. At the local scale, fringing vegetation provides refuge for metamorphs and breeding adults (Hazell, Cunningham, Lindenmayer, Mackey, & Osborne, 2001). Forest loss reduces terrestrial habitat for adults and leads to decreased richness, occurrence and abundance of several amphibian species (Ficetola, Marziali, Rossaro, De Bernardi, & Padoa-Schioppa, 2011; Hamer & McDonnell, 2008). Increased road cover, a surrogate variable for urbanization (Hamer & McDonnell, 2008), may reduce connectivity and isolate populations by limiting dispersal and migration between breeding habitats (Eigenbrod, Hecnar, & Fahrig, 2008; Hitchings & Beebee, 1997).

Urbanization may be an important anthropogenic driver of species loss in terrestrial landscapes, because only a few species able to adapt to rapid urbanization prevail (McDonnell & Hahs, 2015). Thus, management derived from ecological studies in urban landscapes may be biased towards a few common species that are recorded in sufficient numbers to perform statistical analysis. If management of landscapes under high human pressure is based on findings from

these species, it may fail to cater for the needs of species at a higher risk of decline – such as previously common species that become locally-extinct or infrequently encountered as a result of habitat modification (Gaston & Fuller, 2007).

Increased urbanization of natural and rural lands can pose a serious threat to amphibians. However, our ability to guide conservation efforts remains limited because amphibians are among the least studied vertebrate groups in urbanizing landscapes (McDonnell & Hahs, 2008). Although the number of studies of amphibians in urban areas and in landscapes under urban development is growing, planners and managers still lack information to effectively guide amphibian conservation in most urbanizing landscapes worldwide (but see Calhoun, Jansujwicz, Bell, & Hunter, 2014).

To provide conservationists, managers and urban planners with empirical insights to guide effective conservation of common and infrequently encountered amphibian species in urbanizing landscapes, we studied the distribution of pond-breeding frogs during the breeding season in a landscape comprised of forests, rural, and urban areas in southeastern Australia. Population growth and increased demand for holiday houses is triggering forest clearing for urban development in the region, but little is known about how this development affects the native fauna of the area. Currently, it is not known whether local environmental attributes or landscape context are the key factors that influence amphibian communities. The uncertain viability of approximately 96% of frog species in this region (State of the Environment 2011 Committee, 2011) demands urgent insights on the effects of urbanization on frogs to guide conservation

actions. We asked: How is the distribution of pond-breeding frogs during the breeding season influenced by aquatic variables (water body size, aquatic vegetation, and presence of fish), and terrestrial variables (local habitat structure, and, at two spatial scales, forest and road cover)? In particular, we aimed to answer the following three key research questions:

Q1. Are common species (occurrence $\geq 36\%$ of surveyed ponds) influenced by aquatic habitat, terrestrial habitat, or both? This knowledge will allow us to plan and manage urban areas to maintain common species.

Q2. What are the main factors (from the aquatic and terrestrial environments) influencing species richness of infrequently encountered pond-breeding frogs? If infrequently encountered frogs (occurrence $< 35\%$ of surveyed ponds) are influenced by local-scale variables, conservation strategies can aim to improve local habitat condition within urban areas; whereas if they are sensitive to landscape variables, maintaining undisturbed habitat around breeding sites will be important to prevent species loss in urbanizing landscapes.

Q3. Does species richness reflect the variables influencing both common and infrequently encountered species? This is important because frog species richness has been proposed as a focus for conservation management in Australian urban environments (e.g., Hamer & Parris, 2011).

Knowledge of which variables from the aquatic and terrestrial environment influence amphibian distributions in urbanizing landscapes will help guide management and urban planning to conserve both common and infrequently encountered species. This knowledge is essential for amphibian conservation in forest ecosystems undergoing urban development worldwide.

2. Methods

2.1. Study area

This study was conducted between Nowra (34.86°S 150.60°E) and Booderee National Park (35.16°S 150.73°E), and covered approximately 600 km² in New South Wales, southeastern Australia (Figure 1). The study area is dominated by native eucalypt forests and wetlands, and rural and urban areas. Rural areas comprised cleared areas for livestock paddocks. Urban areas comprised several small towns of <10,000 inhabitants and the Nowra-Bomaderry urban center of ~35,000 inhabitants (Australian Bureau of Statistics, 2011). The region has a temperate climate, with warm summers and mild winters. Annual mean minimum and maximum air temperatures are 13.8°C and 20°C, respectively. Annual rainfall is approximately 1,000 mm and is spread evenly throughout the year (www.bom.gov.au).

2.2. Study design

2.2.1. Pond selection

To study the factors which influence frog richness and individual frog species occurrence in ponds with long hydroperiods (flooded for most part of a breeding season), we visually identified and manually digitalized ponds on a Quickbird image (2008, Google EarthTM) at a resolution of 1:2,000. Ponds were stratified based on three land cover types (forest, rural, and urban) to sample ponds in different urbanization levels (McDonnell & Hahs, 2008), and three water body sizes (\leq 50 m, 51-100 m and >100 m in diameter). Land cover type was defined by the land cover

immediately surrounding the pond. Forest cover comprised forests and woodlands within public and private land, rural cover comprised cleared areas for livestock paddocks, and urban cover comprised residential areas and urban parks within towns and the Nowra-Bomaderry urban center. We randomly selected ten ponds within each land cover type and ensured that different water body sizes (≤ 50 m, 51-100 m and >100 m in diameter) were represented (Figure 1). Due to problems with access and vandalism, two sites were not surveyed in urban areas (total ponds surveyed= 28; forest= 10, rural= 10, and urban= 8). All ponds were located >800 m from each other, which we considered sufficient to reduce autocorrelation because most frog species in our study area were unlikely to travel longer distances during a breeding season (Hamer & Parris, 2011; Lauck, 2005).

2.2.2. Pond-breeding frog surveys

In our region, most frog species are easily detected by male calls during the breeding season (e.g., November-February; Amphibian Research Centre, 2012; Lemckert & Mahony, 2008). Although the probability of detecting a frog species at a site can vary within this peak calling activity period, southeastern Australian frogs can be detected at a high rate by using nocturnal aural surveys. For example, Parris (2006) estimated a high (74-99%) probability of detecting a frog species present in a pond with three visits. Therefore, we recorded frog calls at ponds during the breeding season to maximize detectability. Ponds were surveyed in November 2012 and again in January-February 2013. In each survey period, we recorded frog calls over three nights at each pond. For this, we placed an automatic recorder (FaunatechTM, Bairnsdale, Victoria) at a pond edge, which recorded four three-minute blocks per night (total recorded time per pond = 36 min).

Each night, recording started at 21:00, 23:00, 01:00 and 03:00 (Smallbone, Luck, & Wassens, 2011). To avoid confounding the effects of weather with our predictor variables, we surveyed ponds of several sizes and different land cover types simultaneously. We identified species by their calls using reference libraries (e.g., Amphibian Research Centre, 2012).

2.2.3. Aquatic and terrestrial variables

We measured aquatic and terrestrial variables considered likely to affect frog distributions. Aquatic variables included water body size, percentage cover of surface vegetation (sum of emergent and floating vegetation) and presence of eastern gambusia (*Gambusia holbrooki*)—an exotic fish species that can negatively affect frog populations (Shulse et al., 2013) (Table 1). We estimated water body size and surface vegetation cover visually, but calculated water body size in ArcGIS (ESRI) when ponds exceeded 50 m in diameter to increase accuracy of assessment. To detect the presence of eastern gambusia, we performed a five-minute visual search and placed a 1.25-L bottle trap in large ponds or a 0.5-L bottle trap in small (~1.5 m²) ponds for three days (Hamer & Parris, 2011).

Terrestrial variables were quantified at both the landscape and local level. Landscape context variables were calculated using ArcGIS. For each pond, we calculated the total road length (including paved and unpaved roads) within 100 m and 1,000 m buffers using a road shapefile obtained from the Government of New South Wales. In addition, we calculated forest cover within 100 m and 1,000 m buffers surrounding each pond with a raster of forest cover estimated from Landsat satellite images of 2010, 2011 and 2012 (Department of Environment, 2013). At

the local level, we estimated visually within a 10 m buffer from the edge of the water body, the percentage cover of seven habitat types (i.e., bare ground, grassland, shrubland, woodland (tree crowns are clearly separated), forest (tree crowns touching), scattered trees, rocks, and total fringing vegetation) (Table 1). Variables measured at these scales (10 m, 100 m and 1,000 m from the breeding habitat) can influence amphibian distributions and provide important insights to guide planning and development around breeding ponds.

2.3. Data analyses

2.3.1. Detectability of frog species

To determine if our survey effort allowed us to assert that a species was absent with a high degree of confidence, we first calculated the probability of detecting each frog species after a single visit (one day) (MacKenzie et al., 2002) using the 2012 three-day survey data (Scheele et al., 2014). A single-visit detection probability is the probability of detecting the species during a single-visit to a site where the species is present. For each species, we then calculated the cumulative probability of detecting the species following one, two and three-day surveys (Wintle, Kavanagh, McCarthy, & Burgman, 2005).

2.3.2. Predictor aquatic and terrestrial variables

We summarized variation among ponds for terrestrial variables using metric Multidimensional Scaling (MDS) based on Euclidean distances. Each variable was standardized (by subtracting the variable's mean value and dividing by the variable's mean absolute deviation) before calculating

the dissimilarities and a 2-dimensional configuration was used to summarize the data. We did not include road length within 100 m and 1,000 m in the MDS so we could explore their effects separately. This was because road length around ponds can be used as a surrogate variable for urbanization (Hamer & McDonnell, 2008). The first MDS axis described a gradient from ponds characterized by low forest cover within 10 m, 100 m, and 1,000 m and fringing vegetation dominated by grasslands (urban ponds, lower scores), to ponds surrounded by high forest cover within 10 m, 100 m and 1,000 m (forest ponds, higher scores) (Figure 2, Table 1). Thus, the first MDS axis arranged ponds according to urbanization levels: urban, rural and forests (Figure 2). Increasing scores in the second MDS axis characterized ponds with more grassland and less bare ground and rocks within the 10 m buffer, as well as less forest cover within 1,000 m (Figure 2, Table 1).

2.3.3. Effect of habitat variables on frog distributions

We examined the effects of aquatic variables, terrestrial MDS axes and road lengths on total species richness, species richness of infrequently encountered species (detected at <35% of surveyed ponds), and individual species occurrences using model selection with Generalized Linear Models (GLMs) (see sections 2.3.3.1-3). To improve model fit, we transformed predictor variables when needed (Table 1). We confirmed the lack of collinearity between our predictor variables by calculating a correlation matrix and variance inflation factors (VIF; Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Low collinearity ($r \leq 0.5$, VIF <1.6) between predictor variables allowed us to explore their effects separately. We fitted a series of models that included

different combinations of the additive effects of: the three aquatic variables, the two axes from MDS from terrestrial variables, and road length within the 100 m buffer and the 1,000 m buffer.

2.3.3.1. *Models for species richness*

We analyzed total species richness by fitting GLMs with a Poisson distribution (log link). In addition to additive effects, we allowed the first MDS of terrestrial variables to interact with road length within 1 km. In this way, we could distinguish whether the effect of road length within 1 km on species richness was dependent on the amount of forest cover. All models predicting total species richness included the natural logarithm of the number of surveys as an offset to account for different sampling effort in five of our 28 ponds evaluated (which had one instead of two three-day surveys due to limited access and vandalism). To avoid over parameterizing models, we limited the number of variables to be included in the same model to two, but we also included a model with the interactive effect of the first MDS axis with road length within 1 km, and their main effects. Thus, the candidate set for total species richness included 30 models (Supplementary Material, Table S1).

2.3.3.2. *Models for species richness of infrequently encountered species*

We also explored relationships between our predictor variables and species richness of infrequently encountered species. We defined ‘infrequently encountered’ species as those present at <35% of surveyed ponds (i.e., <10 ponds; Table 2). Low occurrence of infrequently encountered species did not allow individual species analysis – given that at least ten detections

(or events) are recommended to model one predictive variable in a logistic regression (e.g., Peduzzi, Concato, Kemper, Holford, & Feinstein, 1996). A histogram revealed many ponds without infrequently encountered species (zero inflation). Thus, we fitted candidate models with negative binomial GLMs and included the natural logarithm of the number of surveys as an offset (Zuur et al., 2009). Given the limited number of ponds with species richness of infrequently encountered species larger than zero ($n = 14$ ponds), we restricted the number of predictor variables in a model to two. Thus, the candidate model set for infrequently encountered species richness comprised 29 models (Supplementary Material, Table S1).

2.3.3.3. *Models for individual species occurrence (common species)*

We defined ‘common’ species as those detected at $\geq 36\%$ of surveyed ponds (≥ 10 ponds; Table 2). Once we confirmed that our common species were detected with a high degree of confidence after three-day surveys (see section 2.3.1), we fitted GLMs with a binomial distribution (logit link) describing the probability of occurrence of individual species. We used the proportion of occurrence of a species in a pond (e.g., for ponds with two surveys (November and January-February): 0= not recorded, 0.5= recorded in one survey, 1= recorded in both surveys) and the number of surveys over which the proportion of occurrence was calculated was modeled as model weights (binomial glm, R Core Team, 2013). To minimize the number of models we fit, we did not include the second MDS axis (because it was less biologically meaningful than the first MDS axis) and we restricted the inclusion of predictor variables to two within a model. This led to 22 models in the candidate set for each species (Supplementary Material, Table S1).

2.3.3.4. Model selection

We selected the best GLMs from each candidate model set (i.e., total species richness, species richness of infrequently encountered species and individual species occurrence) using an information-theoretic approach, based on Akaike's Information Criterion corrected by small sample size (AICc) (Burnham & Anderson, 2002). We first assessed overdispersion in models fitted with all our predictor variables for each response variable. We did this by comparing the model residual with the residual degrees of freedom. Only GLMs fitted for *Litoria fallax* occurrence showed evidence of overdispersion and thus, models for this species were selected with Quasi-AICc (QAICc) instead of AICc (Burnham & Anderson, 2002). From the set of top-ranked models (those within 2-AICc or 2-QAICc units from the best model), we disregarded models with uninformative parameters. Models with uninformative parameters are those within 2 AICc-units of a better-ranked model that include one parameter in addition to parameters in the better model. In those circumstances, the new parameter does not explain enough variation to justify its ecological interpretation (Arnold, 2010). Finally, we predicted the individual effect of each explanatory variable from our 'best' models (lowest AICc or QAICc) for each response variable.

All statistical analyses were performed in R-3.0.1 (R Core Team, 2013). We used the function *glm.nb* in the package "MASS" (Venables & Ripley, 2002) for fitting negative binomial GLMs; "unmarked" for detectability analyses (Fiske & Chandler, 2011); "MuMIn" (Barton, 2013) for model selection; and the functions *cmdscale* and *predict.glm* in the package "stats" for

calculating MDS and to obtain predicted values and standard errors from best models,
 respectively (R Core Team, 2013).

3. Results

We recorded 14 frog species at 28 ponds (Table 2). All were native species and one (*L. aurea*) is endangered under state-level legislation (NSW Threatened Species Conservation Act 1995). Five species were recorded in a sufficient number of ponds to allow individual species analysis: *Crinia signifera* (71% of ponds), *L. peronii* (71%), *Limnodynastes peronii* (*Lim. peronii* from now on; 46%), *Litoria fallax* (43%) and *L. tyleri* (36%). Among these common species, the probability of detecting a species on any single visit was highest for *L. fallax* (Estimate \pm SE = 0.97 ± 0.03) and lowest for *Lim. peronii* (0.57 ± 0.13). After a three-day survey, the probability of detecting the species with lowest detection (*Lim. peronii*) was 0.92 (95% CI= 0.83-0.97; Appendix, Figure A). For infrequently encountered species (detected at $\leq 21\%$ of ponds), the probability of detecting a species with a three-day survey was high, ranging from 0.95 to 0.99 (95% CI= 0.79-0.99); except for *Pseudophryne bibronii* (0.04, 95% CI= 0-0.1). *Pseudophryne bibronii* is one of the few frog species that breeds during autumn in our region (e.g., March-June; Amphibian Research Centre, 2012) so was not expected to be adequately sampled in our study. Exploratory analyses showed that predictor terrestrial variables varied with urbanization levels, but there was no evidence of bias for predictor aquatic variables in relation to urbanization levels (Supplementary Material, Figures S1-S2).

3.1. Species richness

Total species richness recorded at a pond varied from zero to nine species (median = 3.5 species); whereas species richness of infrequently encountered species recorded at a pond varied from zero to five species (median = 0.5 species). The best model for total species richness contained two explanatory variables: the natural logarithm of water body size ($\beta_1 = 0.14 \pm 0.05$, $P=0.01$) and the natural logarithm of road length within 1km ($\beta_2 = -0.45 \pm 0.16$, $P=0.006$; Table A, Figure 3A). That is, there was a positive effect of increasing water body size on total species richness that was most important at small pond sizes and a decline in total species richness with increasing road length within 1 km (Figure 3A).

Species richness of infrequently encountered species also declined with increased road length within 1 km, but at a higher rate than total species richness ($\beta_2 = -1.13 \pm 0.37$, $P=0.002$; Table A, Figure 3B). The natural logarithm of road length within 1 km was an important predictor for species richness of infrequently encountered species, because it was present in the two competitive models (within $2\text{-}\Delta\text{AICc}$, Table A). In addition, species richness of infrequently encountered species increased with the first MDS axis ($\beta_1 = 0.2 \pm 0.1$, $P=0.048$) and thus, it was highest in ponds within forests (positive values for terrestrial MDS-1; Figure 3B). To confirm that the influence of landscape variables (roads within 1 km) on total species richness were due to their influence on infrequently encountered species rather than on common species, we performed a supplemental model selection to evaluate the influence of terrestrial and aquatic variables on common species richness. Our supplemental analysis confirmed that the natural logarithm of water body size was the main variable influencing common species richness

(Supplementary Material, Table S2). Thus, the influence of roads within 1 km from breeding ponds on total species richness is due to the negative influence of terrestrial variables on infrequently encountered species.

3.2. Individual species occurrence

The best models for individual species occurrence revealed that the probability of occurrence for *C. signifera*, *L. peronii* and *L. tyleri* increased with the natural logarithm of water body size (Table A, Figure 3C-E). The likelihood of recording *C. signifera* increased with increasing percentage of aquatic vegetation ($\beta_2 = 0.205 \pm 0.1$, $P=0.04$, $\Delta AICc = 0$), although the null model was included among the best models ($\Delta AICc = 1.77$; Table A; Figure 3C). *Litoria peronii* occurrence in ponds surrounded by >100 m road length was lower than in ponds surrounded by <100 m road length within 100 m buffer ($\beta_2 = -1.45 \pm 0.65$, $P=0.03$; Table A; Figure 3D). *Limnodynastes peronii* occurrence increased in ponds with a higher percentage cover of aquatic vegetation ($\beta_1 = 0.33 \pm 0.11$, $P=0.003$; Table A; Figure 3F). The best model describing *L. fallax* occurrence was the null model (Table A).

4. Discussion

To help guide management and land use planning for amphibian conservation in urbanizing forested landscapes, we examined the relative importance of aquatic and terrestrial variables for

pond-breeding frogs during a breeding season in a landscape of forests, rural and urban areas. In line of the three key questions posed at the Introduction, we found:

(1) The occurrence of common frogs was best explained by the local (aquatic) habitat.

(2) The richness of infrequently encountered frog species was best predicted by the terrestrial environment at a large spatial scale, implying that habitat modification as far as 1 km from breeding habitats may be the key driver of local species loss rather than local-scale modification of individual breeding sites.

(3) Total species richness captured the influence of local habitat on common species as well as landscape variables on infrequently encountered species. But at the species richness level, common species attenuated the steep decline of infrequently encountered species with increasing road length within 1 km from breeding ponds.

Our findings suggest that management of local habitat may help conserve a few common frog species, but it will fail to conserve many frog species disadvantaged by urbanization of the broader landscape. We discuss the influence of aquatic and terrestrial environments on our pond-breeding frogs. In addition, we suggest that conservation guidelines should integrate local-scale management of aquatic habitats and land use planning to maintain both common and infrequently encountered frog species in urbanizing landscapes.

4.1. Local aquatic environment and amphibian distribution

Larger ponds supported higher frog species richness than smaller ponds, and had a greater probability of supporting common species (i.e., recorded at $\geq 36\%$ of surveyed ponds, such as *C.*

signifera, *L. peronii* and *L. tyleri*). However, the benefits of increasing water body size on species richness and the occurrence of common species was more important at small pond sizes (e.g., <500 m²; Figure 3). Greater frog species richness with increasing water body size, as well as the greater benefits of increasing water body size at small pond sizes, agrees with findings from other work in our study area (Westgate, Driscoll, & Lindenmayer, 2012), elsewhere in Australia (Parris, 2006) and worldwide (for a review, see Hamer & McDonnell, 2008). Some frog species benefit from larger water bodies due to longer hydroperiods, which might provide breeding habitat for a longer time within a breeding season (Westgate et al., 2012). In addition, larger ponds may support higher species richness because they provide a variety of niches and also can support larger populations, reducing extinction rates (Hanski, 1994; Parris, 2006).

Aquatic vegetation had a limited effect on most frog species. However, it was the most important variable predicting *Lim. peronii* occurrence. For instance, it was very unlikely to find *Lim. peronii* in ponds with no surface vegetation (95% CI: 0.02-0.28), but ponds with 80% of surface vegetation were more likely to support *Lim. peronii* (95% CI: 0.41-0.79). *Limnodynastes peronii* has large egg masses (Table 2) that it lays in floating foam nests concealed in surface vegetation (Anstis, 2007). Thus, aquatic vegetation may provide suitable conditions for *Lim. peronii* to lay eggs, as well as refuge against predation for both adults and larvae, helping this species to persist in urban landscapes and colonize a variety of urban ponds (Amphibian Research Centre, 2012). We recorded this species in small urban garden ponds, which reveals its tolerance of small breeding habitats, forest fragmentation and residential development compared to other frogs in our study area.

4.2. Terrestrial environment and amphibian distribution

The terrestrial variables we measured had limited effects on the occurrence of most common frog species, except for *L. peronii*. *Crinia signifera*, *Lim. peronii*, *L. peronii*, *L. tyleri* and *L. fallax* are widespread species that can tolerate some level of disturbance (Table 2). However, *L. peronii* was sensitive to urbanization: *L. peronii* was less likely to occur in ponds surrounded by >100 m road length within 100 m buffer. Despite the positive associations of the genus *Litoria* with increased urbanization found elsewhere in Australia (Hamer & Parris, 2011), we found *L. peronii* was sensitive to urbanization within 100 m from breeding ponds.

Urbanization at large spatial scales (within 1 km of ponds) had negative effects on species richness. Ponds with less surrounding forest and higher road cover within 1 km supported fewer infrequently encountered frog species. Thus, species richness of infrequently encountered species was highest in forest ponds, lower in rural ponds and lowest in urban ponds (Figure 3B). In addition, the number of infrequently encountered frog species at a pond declined strongly with small increases in the surrounding road length. This agrees with findings from other urban studies, where breeding sites surrounded by limited forest cover and a large number of roads supported low frog species richness (Hamer & McDonnell, 2008; Parris, 2006; Simon, Snodgrass, Casey, & Sparling, 2009). However, the steep rate of decline of infrequently encountered frogs with small increases in road cover within 1 km was subdued at the species richness level, demonstrating that biodiversity metrics like total species richness may underestimate the impacts of urbanization.

434

435 Our findings for infrequently encountered species suggest urbanization is the key factor driving
436 loss of pond-breeding frogs in our region. Urbanization can increase extinction risk of frog
437 populations due to increased mortality on roads and can limit colonization of potential breeding
438 ponds due to increased isolation (Hitchings & Beebee, 1997; Rytwinski & Fahrig, 2015). In
439 addition to increased mortality on roads, greater isolation in urban landscapes may be caused by
440 physical barriers (e.g., buildings, fences) and behavioral barriers (e.g., avoidance of impervious
441 surfaces or traffic disturbance) (Eigenbrod et al., 2008; Rytwinski & Fahrig, 2015). Maintaining
442 breeding habitat within large expanses of undisturbed forest can help frog populations persist by
443 providing terrestrial habitat for juveniles and adults (e.g., upland and non-breeding habitat),
444 maintaining local migratory routes between breeding and non-breeding habitats, and promoting
445 connectivity among populations (Hamer & McDonnell, 2008).

446

447 Although we examined only one breeding season, we expect the patterns of occurrence of
448 common and infrequently encountered species we quantified to reflect longer term trends. Other
449 studies have reported the importance of similar variables to those identified in this study which
450 influence frog species richness within our study area (in reserves, Westgate et al., 2012) and in
451 other parts of south-eastern Australia (in urban areas, Hamer & Parris, 2011; Parris, 2006;
452 Smallbone et al., 2011). In addition, ‘normal weather’ conditions were recorded for surveyed
453 years. Annual rainfall >1,000 mm has been recorded in our study area after 2010 (at Sanctuary
454 Point station; www.bom.gov.au), following a dry year in 2009 (713.2 mm). Although we expect

some changes to occur over time, we believe the patterns observed in our study are unlikely to be an annual anomaly.

4.3. Amphibian conservation in urbanizing landscapes

Our findings highlight that to achieve the conservation of both common and infrequently encountered species in urbanizing forested landscapes, planners must look at both local breeding habitats and the surrounding landscape. Most policies relating to frog conservation focus on immediate habitats surrounding breeding habitats (Calhoun et al., 2014; Semlitsch, 2000). However, our study revealed that decreasing forest cover (at different spatial scales) and increasing road cover within 1 km of ponds reduces the occurrence of infrequently encountered frog species. This mismatch between the scale at which environmental policies define restrictions for development and the scale at which development has detrimental effects on habitat quality for several species raises concern in this study system, and in others (Calhoun et al., 2014; Harper, Rittenhouse, & Semlitsch, 2008; Semlitsch, 2000).

How can we conserve frog species in urbanizing landscapes? Our findings suggest that in landscapes dominated by forests and where most development leads to the creation or expansion of small urban centers (e.g., <10,000 inhabitants), common frogs could travel across terrestrial habitats and inhabit suitable ponds. Conservation of common frogs in these kinds of urban areas may therefore be improved by appropriately managing aquatic habitats. For instance, increasing the water body size of small ponds may benefit frog species richness, as well as the occurrence of *C. signifera*, *L. peronii* and *L. tyleri*. Our species-area curves for common species also suggest

that adding or retaining several medium-size (e.g., ~500-5,000 m²) ponds may result in a greater gain in occurrence or species richness of common species than adding or retaining fewer but larger (e.g., >5,000 m²) ponds. In addition, managing ponds so they develop a high percentage of surface vegetation may increase *Lim. peronii* occurrence; whereas avoiding road development within 100 m of a pond can increase the likelihood of maintaining *L. peronii*. These few common species tolerate some level of disturbance and may colonize new ponds or wetlands within rural and urban areas (Lauck, 2005; Parris, 2006); which provides opportunities for conservation of common native species in urban environments as well as environmental education and awareness (Compton, McGarigal, Cushman, & Gamble, 2007).

Our results on species richness of infrequently encountered species add to the evidence that urbanization has negative impacts on amphibians. To conserve infrequently encountered frog species at a landscape scale, it is necessary to preserve undisturbed natural vegetation cover within long distances from breeding habitats (1 km in our study). Maintaining ponds within a system of connected reserves may help to reduce the impacts of habitat loss and urbanization on breeding sites, while providing terrestrial habitat and permeable migratory routes (Compton et al., 2007; Harper et al., 2008). Furthermore, because amphibians are particularly susceptible to habitat fragmentation by roads and direct mortality on roads (Rytwinski & Fahrig, 2015), careful planning and mitigation strategies are needed to reduce road impacts (e.g., fences to direct amphibians to safe passages; Cosentino et al., 2014).

Contrasting responses by common and infrequently encountered frog species highlight the need for management and planning at both local and landscape scales. Incorporating these approaches into policy and practice will require local guidelines for amphibian conservation, long-term monitoring studies and multidisciplinary efforts (Calhoun et al., 2014). For instance, in the USA, local guidelines for forestry and urban development (e.g., best development practices; Calhoun, Nicholas, & Klemens, 2005); as well as local solutions to conserving pool landscapes (Calhoun et al., 2014) have been established to maintain amphibian populations and their habitats in the face of urbanization. In addition, tools for spatial planning (e.g., Baldwin & deMaynadier, 2009) can help to integrate scientific evidence into landscape planning for amphibian conservation.

5. Conclusions

What are the variables from aquatic and terrestrial environments that common and infrequently encountered species respond to? The key discovery in this study was that during the breeding season, common frogs responded to local aquatic variables (pond size and surface vegetation) whereas infrequently encountered frog species were highly sensitive to modification of the broader terrestrial environment. Managing ponds for appropriate water body size and a high percentage cover of surface vegetation may increase species richness by increasing the occurrence of common species, but it will not prevent the decline of many species that respond to modification of terrestrial habitats as far as 1 km from breeding ponds. Therefore, to conserve both common and infrequently encountered pond-breeding frogs, we suggest:

519 (1) for common frogs (that tolerate urbanization), manage ponds to provide suitable habitat
520 within rural and urban areas;

521 (2) for infrequently encountered frogs (sensitive to urbanization), maintain a connected reserve
522 system to limit deforestation, road development and urbanization within large areas surrounding
523 breeding ponds, and mitigate the impacts of urbanization on remaining populations (e.g., road
524 mitigation measures); and

525 (3) for all amphibians, formulate local best development practices, undertake spatial planning,
526 and establish long-term monitoring to better integrate effective amphibian conservation practices
527 into urban planning and land use policies.

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List of tables

Table 1. Aquatic and terrestrial habitat variables explored in southeastern Australia. For terrestrial variables, correlations between metric Multidimensional Scaling (MDS) axes and habitat variables are shown. MDS-1= first axis from MDS; MDS-2= second axis from MDS. Correlations >0.5 are shown in bold.

Table 2. Life history characteristics of frog species recorded in southeastern Australia. For each species, habitats, averaged numbers of eggs per female, proportion of sites where each species was recorded as present in our study and whether a species was considered common or infrequently encountered are shown. Common species allowed individual species analyses (present at $\geq 36\%$ of ponds).

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Type of environment	Variable	Unit	Range	Transformation	Correlations	
					Terrestrial	
					MDS-1	MDS-2
Aquatic	water body size	m ²	2-25,213	ln		
	surface vegetation	%	0-100	squared root		
	presence of gambusia		0,1			
Terrestrial	- landscape context					
	road length within 100 m buffer	m	0-860	binary [<100, ≥100]		
	road length within 1,000 m buffer	km	3.4-35.5	ln		
	forest cover within 100 m buffer	ha	0-3.1	standardized	0.88	-0.06
	forest cover within 1,000 m buffer	ha	7.1-313.1	standardized	0.61	-0.6
	- habitat structure at local scale (10 m buffer)					
	fringing vegetation	%	28-100	standardized	0.62	0.47
	bare ground	%	0-65	standardized	-0.25	-0.53
	grassland	%	0-100	standardized	-0.63	0.55
	shrubland	%	0-75	standardized	-0.22	-0.3
	woodland	%	0-98	standardized	0.45	-0.3
	forest	%	0-100	standardized	0.64	0.03
	scattered trees	%	0-44	standardized	-0.15	0.49
	rocks	%	0-23	standardized	-0.5	-0.62

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Species	Common name	Habitats	Averaged no. of eggs	Proportion of sites	Type
<i>Crinia signifera</i>	Common Eastern Froglet	Widespread	216	0.71	common
<i>Litoria peronii</i>	Peron's Tree Frog	F, W, C, U	1,777	0.71	common
<i>Limnodynastes peronii</i>	Brown-striped Frog	Widespread	1,319	0.46	common
<i>Litoria fallax</i>	Eastern Dwarf Tree Frog	Widespread	283	0.43	common
<i>Litoria tyleri</i>	Tyler's Tree Frog	F, C	>128	0.36	common
<i>Litoria jervisiensis</i>	Jervis Bay Tree Frog	F, H, Sw	920	0.21	infrequently encountered
<i>Litoria verreauxii</i>	Verreaux's Frog	F, H, C, near U	725	0.21	infrequently encountered
<i>Uperoleia sp.</i>	-	F, W, C	?	0.18	infrequently encountered
<i>Paracrinia haswelli</i>	Haswell's Froglet	W, H, S	188	0.14	infrequently encountered
<i>Litoria freycineti</i>	Freycinet's Frog	H, Sw	478	0.07	infrequently encountered
<i>Limnodynastes dumerilii</i>	Eastern Banjo Frog	F, W, H, C	3,900	0.04	infrequently encountered
<i>Litoria aurea</i>	Green and Golden Bell Frog	F, W, Sw	5,121	0.04	infrequently encountered
<i>Litoria dentata</i>	Bleating Tree Frog	S	1,070	0.04	infrequently encountered
<i>Pseudophryne bibronii</i>	Bibron's Toadlet	F, H, C	163	0.04	infrequently encountered

Habitat: F= Forest; W = Woodland; H = Heathland, S = Shrubland; Sw = Swamps; C = cleared; U = Human settlements (source: Anstis, 2007; Tyler, 1998).

List of figures

Figure 1. Study area showing 28 surveyed ponds located in an urbanizing forested landscape in southeastern Australia. Forest cover and road network are also shown. Note that symbols representing ponds may hide the land cover type immediately surrounding a pond.

Figure 2. Metric Multidimensional Scaling (MDS) of terrestrial variables associated to wetlands in south-eastern Australia. Symbols represent land cover type: (●) forests, (○) rural areas; and (▲) urban settlements. Variables correlated ($r > 0.5$) to each axis are shown, with subscripts representing the spatial scale. See Table 1 for details about correlations between variables.

Figure 3. Estimated species richness and individual species occurrence in Generalized Linear Models (GLMs) from model with highest support (lowest AICc). Estimated (A) total species richness in GLMs with a Poisson distribution (log link) and (B) species richness of infrequently encountered species in negative binomial GLMs. Estimated probability of occurrence for (C) *C. signifera*, (D) *L. peronii*, (E) *L. tyleri*, and (F) *Lim. peronii* in GLMs with a binomial distribution (logit link). Shadows represent confidence intervals at a 95% confidence level.

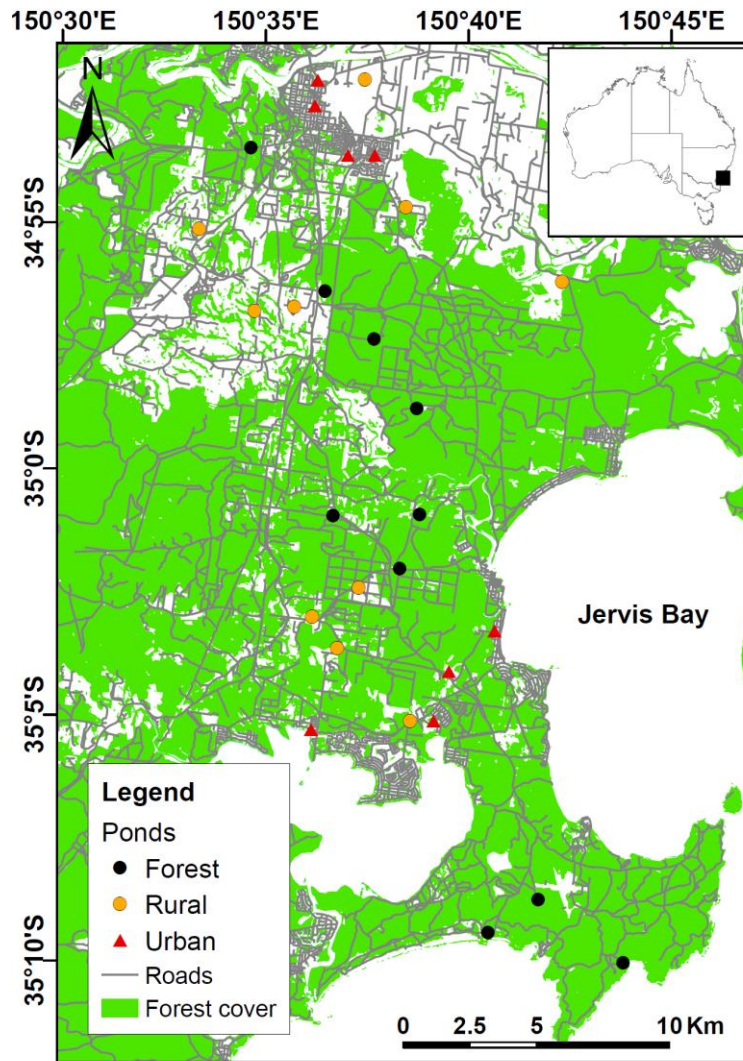


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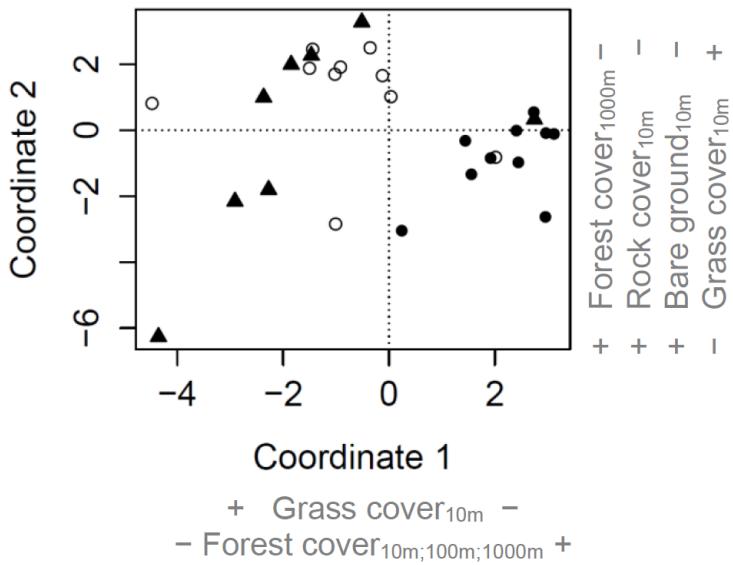


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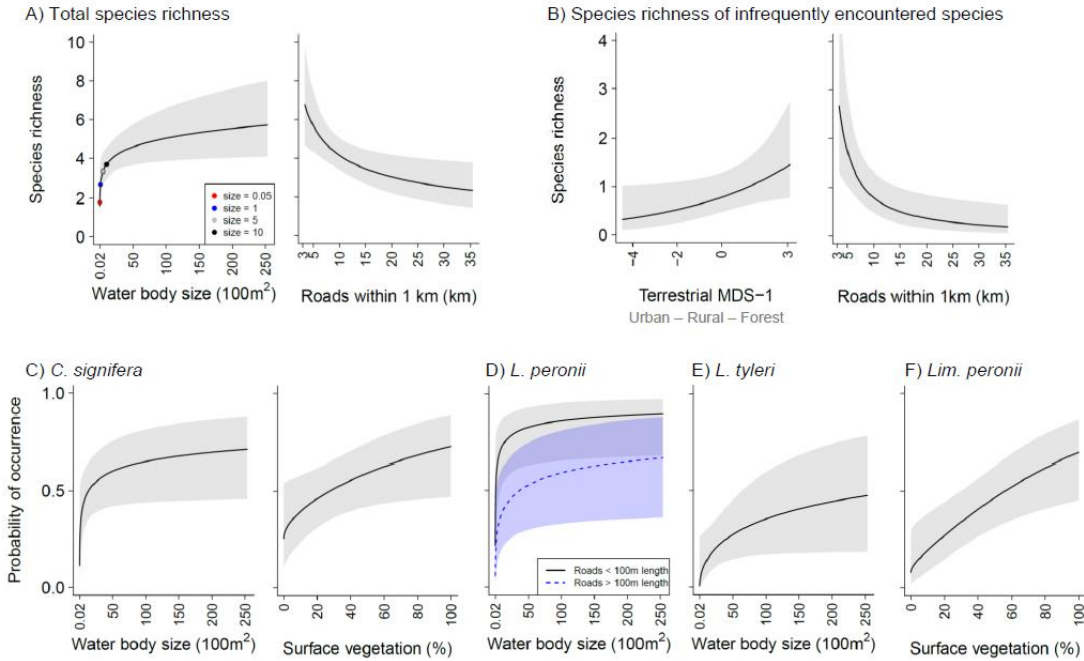


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List of appendices

Figure A. Probability of detection for A) *C. signifera*, B) *L. peronii*, C) *L. fallax*, D) *L. tyleri*, and E) *Lim. peronii* recorded in southeastern Australia. Estimates are based on single-visit detection probabilities from 2012 data. Vertical lines represent 95% CI. After three days, all species reached 0.9 detection probability (dashed line).

Table A. Variable estimates from the best models selected by bias corrected Akaike Information Criterion (AICc) for species richness and five individual species occurrences. Model selection was performed on Generalized Linear Models (GLMs) with a Poisson distribution (log link) for total species richness, negative binomial for species richness of infrequently encountered species, and a binomial distribution (logit link) for individual species occurrence. ΔAICc shows the difference in AICc between the current model and the model with the highest support (lowest AICc). W (model weight) shows the relative probability of the model being the best model of the entire candidate set. (*) Model with the highest support for each response variable. Models with uninformative parameters were excluded from consideration (see Methods). All models include intercept (number standing alone). Variables included in best models: natural logarithm of water body size = $\ln(\text{water body size})$; square root of surface vegetation (%) = $\sqrt{(\text{surface vegetation})}$; first axis from metric multidimensional scaling (MDS) of terrestrial variables = MDS-1; natural logarithm of road length (km) within 1,000 m buffer = $\ln(\text{roads.1km})$; road.100m = binary variable indicating whether >100 m road length was present within 100 m buffer. Detailed results of model selection are shown in Supplementary Material (Table S1).

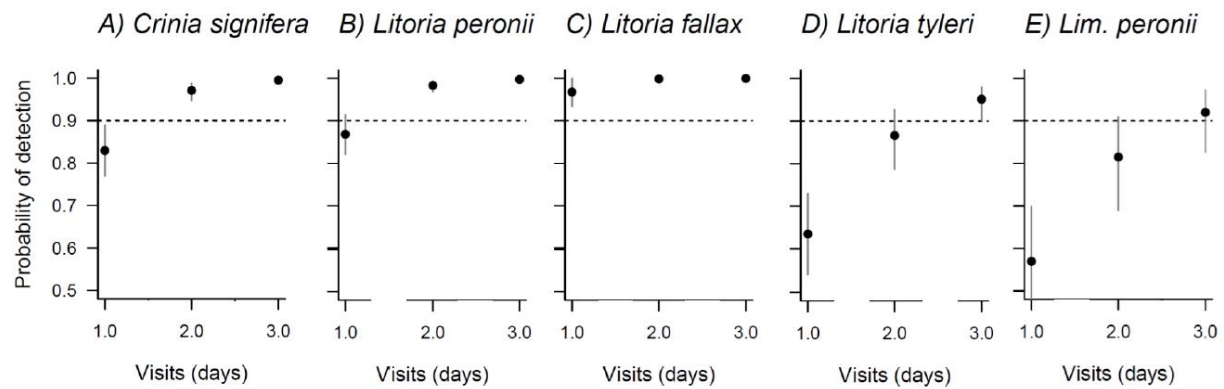


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Response	Model (linear predictors)	logLik	AICc	ΔAICc	W
Total species richness	0.74 + 0.14 $\ln(\text{water body size})$ – 0.45 $\ln(\text{roads.1km})$	-49.80	106.6	*	0.51
Species richness of infrequently encountered species	1.72 + 0.20 MDS-1 – 1.13 $\ln(\text{roads.1km})$	-32.68	75.1	*	0.26
	2.06 – 1.24 $\ln(\text{roads.1km})$	-34.52	76.0	0.94	0.16
<i>C. signifera</i>	–3.47 + 0.32 $\ln(\text{water body size})$ + 0.20 $\sqrt{(\text{surface vegetation})}$	-24.79	56.6	*	0.18
	–2.0 + 0.27 $\ln(\text{water body size})$	-26.35	57.2	0.61	0.13
	–1.01 + 0.16 $\sqrt{(\text{surface vegetation})}$	-26.90	58.3	1.71	0.08
	–0.12	-28.10	58.3	1.77	0.07
<i>L. peronii</i>	–1.56 + 0.37 $\ln(\text{water body size})$ – 1.45 roads.100m	-23.02	53.0	*	0.35
<i>Lim. peronii</i>	–2.46 + 0.33 $\sqrt{(\text{surface vegetation})}$	-23.24	51.0	*	0.28
<i>L. tyleri</i>	–5.62 + 0.54 $\ln(\text{water body size})$	-14.84	34.1	*	0.27
<i>L. fallax</i> ¹	–0.4	-32.78	36.3	*	0.15

¹ Model selection for *L. fallax* was performed with Quasi-AICc (QAICc) to account for overdispersion (see Methods).